



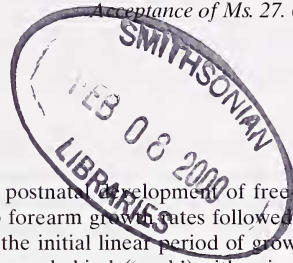
Parturition, parental behaviour, and pup development in Indian false vampire bats, *Megaderma lyra*

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Abstract

This report provides the first observations on parturition and postnatal development of free-ranging Indian false vampire bats. Pup sex ratio was balanced and pup forearm growth rates followed a logistic growth curve. Individuals showed considerable variance in the initial linear period of growth, ranging from 0.53 mm/d to 1.35 mm/d. Females started leaving pups behind ('park') either in the day roost or in special night roosts when pups were between 1 and 23 days old. Possible reasons for both the variability in growth and the onset of leaving pups on their own are discussed. Contact calls in this species consisted of repeated squeaking sounds and were not only emitted by mothers and pups, but also by other false vampires. They occurred most frequently in the morning and evening, during bursts of major activity in the colony.

Key words: *Megaderma lyra*, parturition, postnatal growth, night roosts, contact calls

Introduction

Parturition has been observed only in few bat species (WIMSATT 1960; KUNZ et al. 1994), including one report on captive Indian false vampires (*Megaderma lyra*; GOPALAKRISHNA et al. 1976). To our knowledge, this is the first description on parturition in free-ranging Indian false vampires.

Postnatal growth is an important life-history trait in mammals and represents an important index of maternal input (OFTEDAL and GITTLEMAN 1989). Differences in this early development may affect fitness, such as offspring survival and future reproductive success (e.g. CLUTTON-BROCK 1991; HOFER and EAST 1996). Growth is influenced by environmental variables such as food, temperature, maternal status, and condition. Young bats remain nutritionally dependent on their mothers for a prolonged period of time and female bats provide their young with milk until they achieve at least 90% of adult wing dimension and 70% of adult body mass (KUNZ and STERN 1995). Hence, maternal input (EVANS 1990) should play a crucial role in patterns of postnatal growth before pups achieve flight (BARCLAY 1994). We were interested to find out whether there are individual differences in postnatal growth and maternal attendance during early development of Indian false vampires.

Materials and methods

Caves are natural roosts of Indian false vampires but this species exploits also man-made structures (BROSSET 1962; AUDET et al. 1991; BALASINGH et al. 1994; MARIMUTHU et al. 1995). We investigated a temple-dwelling colony of about 60 false vampires in a small village about 15 km south-east of Tirunelveli (Southern India). Observations were conducted at the beginning of the dry season (February–May 1995), when females are expected to give birth and rear their young (BALASINGH et al. 1994). Maximum outside temperature was $39.1 \pm 2.6^\circ\text{C}$ (mean \pm sd; day, $N = 38$), minimum temperature was $25.9 \pm 1.4^\circ\text{C}$ (night, $N = 38$). Average temperature inside the day roost was rather constant with $32.6 \pm 0.9^\circ\text{C}$ during day ($N = 43$) and $31.2 \pm 0.9^\circ\text{C}$ during night ($N = 43$).

The day roost was continuously illuminated with dim red light (nine 15 W bulbs), which did not seem to disturb the false vampires, as bats often hung close (<20 cm) to the bulbs. False vampires were caught with mistnets during emergence from the roost and removed from the net immediately. Lactating females carrying a pup were released without further handling to avoid injuries to the pup. Other individuals were sexed and weighed. Forearm length was measured to the nearest millimetre. Seventy percent of caught individuals carried a collar and coloured plastic beads from a previous study (BALASINGH et al. 1992). The beads, however, were invisible in most of the cases and only a few bats could be identified from these tags. To improve individual identification we tagged 34 adults ($\sim 50\%$ of the colony) with coloured wing bands (Museum Bonn, Germany, size E). Males were tagged on the left and females on the right forearm. ‘‘Parked’’ pups were tagged by painting either their claws with nail enamel or their ears with non-toxic dye (Marabu). When a pup was hanging alone at a roosting place we measured the right forearm with a pair of vernier callipers while standing on a chair beside the pup. We used the NONLIN function implemented in SYSTAT 5.0 (WILKINSON et al. 1992) to derive an equation for the forearm growth of pups. The equation was calculated combining data from 2 captive (colony in Munich, Germany) and 5 free-ranging false vampires of known age.

Total observation time in the day roost comprised 335 hours. Four other buildings in the vicinity of the temple, where false vampires perched during the night (night roosts) were observed during 105 hours. Night roosts were inspected daily to record whether any pup was ‘‘parked’’ inside the roost. Observations in night roosts were done mainly with a night vision scope supported by stationary red-light torches.

Pup vocalisations were recorded with an electrostatic microphone (Petterson), amplified with an Ultrasonic Detector (Petterson D940), and stored into a Racal Store 4 DS tape recorder with a tape speed of 30 in/s. The recordings were digitised and analysed using a custom-made sound analysis software (Sona, M. Knipschild, Dortmund).

Statistical analyses were conducted with SYSTAT 5.0 (WILKINSON et al. 1992), following the procedures recommended by SOKAL and ROHLF (1995) and LAMPRECHT (1992). The significance level was set as $\alpha = 0.05$ (two-tailed). Data are presented as mean \pm SD or, when skewed, as median/interquartile range.

Results

Parturitions

Female false vampires gave birth to a single pup. The first pup was born on March 17th, the last one on April 18th. After this date no more pregnant females were observed. The total number of pups was about 20. Five females were observed during parturition and another female was seen eating the placenta immediately after parturition. All of these observations occurred between 11.05 h and 12.39 h local time, suggesting that the time around noon could be preferred for parturition (binomial test, $N = 6$, $x = 0$, $p < 0.05$).

During parturition females generally produced a hollow space between abdomen and wings by slightly spreading the wings around the abdomen. One female did not cover her abdomen and we were able to observe the emergence of the pup. At 11.05 h we saw the head and upper breast of the pup emerging out of the vagina. The mother bowed forward and licked the young, especially its head and flanks. At 11.08 h the pup emerged from the vagina. However, its left forearm still stuck to the vagina. The pup revolved round its

forearm and thus got into the position to clasp to its mother in carrying position. Its head was now close to the inguinal nipples and its legs close to the breast of its mother. At 11.16 h the mother stopped licking the pup. Twenty minutes later she started licking again, especially the pup's left flank. She repeatedly pushed her pup's left flank. At 11.38 h the pup's forearm suddenly emerged from the vagina, while the mother was still pushing the pup. The pup slipped slightly downwards and made a squeaking sound. It clasped the neck of the mother with its feet and the mother started to lick the pup's left forearm and, by pushing the pup to one side, her own belly intensively. At 11.45 h the placenta began to emerge, while the mother was still licking her belly. Then she slightly wrapped her wings around her pup. One minute later the mother again began to lick her belly and the pup. Now the placenta left the vagina completely and hung down the umbilical cord. At 11.51 h the mother started to feed on the placenta, which took her 4 minutes. Then she again licked the pup and her own genitals. At 12.05 h the mother wrapped her wings around the pup and rested.

After parturition all mothers licked their pup and their own genital region intensively, the latter may be a support to discharge the placenta. Mothers ate the placenta almost immediately after it had been discharged ($N = 4$, latency of feeding: 1.5/1–2 min, duration of feeding: 3.5/3–4 min).

False vampire pups cling to their mother in the 'carrying-position', venter to venter, the head pointing towards the anus of the mother. With its mouth the pup sucks at one of the two inguinal nipples. These nipples are special attaching warts, no functional teats. The pup wraps its legs around the neck of the mother, crossing them behind her shoulders. The wings are folded at the mother's flank.

When false vampire pups tried to get into this carrying position after birth their mothers assisted them in different ways. Two bats used their muzzles to guide their pups to teats and inguinal nipples. Two other bats made stretching movements while their pups tried to get into the carrying position after birth. Three different pups struggled 10, 20, and 45 minutes until they succeeded in reaching the carrying position. It seemed to be difficult and laborious for the pup, which is delivered head-first to revolve around itself and reach the carrying position. In the carrying position pups frequently lost the sucking grip to an inguinal nipple and the heads suddenly emerged out between the wings of the mothers. The mothers then pushed their pup back with their muzzle. Larger pups frequently hung pendant-like, grasping only the neck of their mother. In this position they stretched their wings, groomed themselves, and did wing flapping.

Sex ratio and growth rates

The sex ratio of identified pups was balanced (6 males and 6 females). The sex of two other pups was not determined. To derive a model for the forearm growth of false vampire pups we combined data of 5 pups (3 females, 2 sex unknown) of known age with data of 2 female pups from a captive colony in Munich. We computed a logistic equation (forearm length = $64.382 \{e^{-0.080(\text{age}+0.697)} + 1\}^{-1}$) which appropriately fitted to the data (corrected $r^2 = 0.97$, Fig. 1). The mean birth forearm length calculated with this equation was 34 mm. During the first 22 days of development the slope of the logistic equation almost equalled the slope of a linear curve (Fig. 1). We took data from 6 individuals for which appropriate data were available for this period and calculated their individual growth rates. Individuals showed considerable variation, ranging from 0.53 mm/d to 1.35 mm/d (Fig. 2). Two pups parked in night roosts (Fig. 2, individuals no. 2 and 3) had relatively low growth rates, but the sample size does not allow a meaningful statistical comparison.

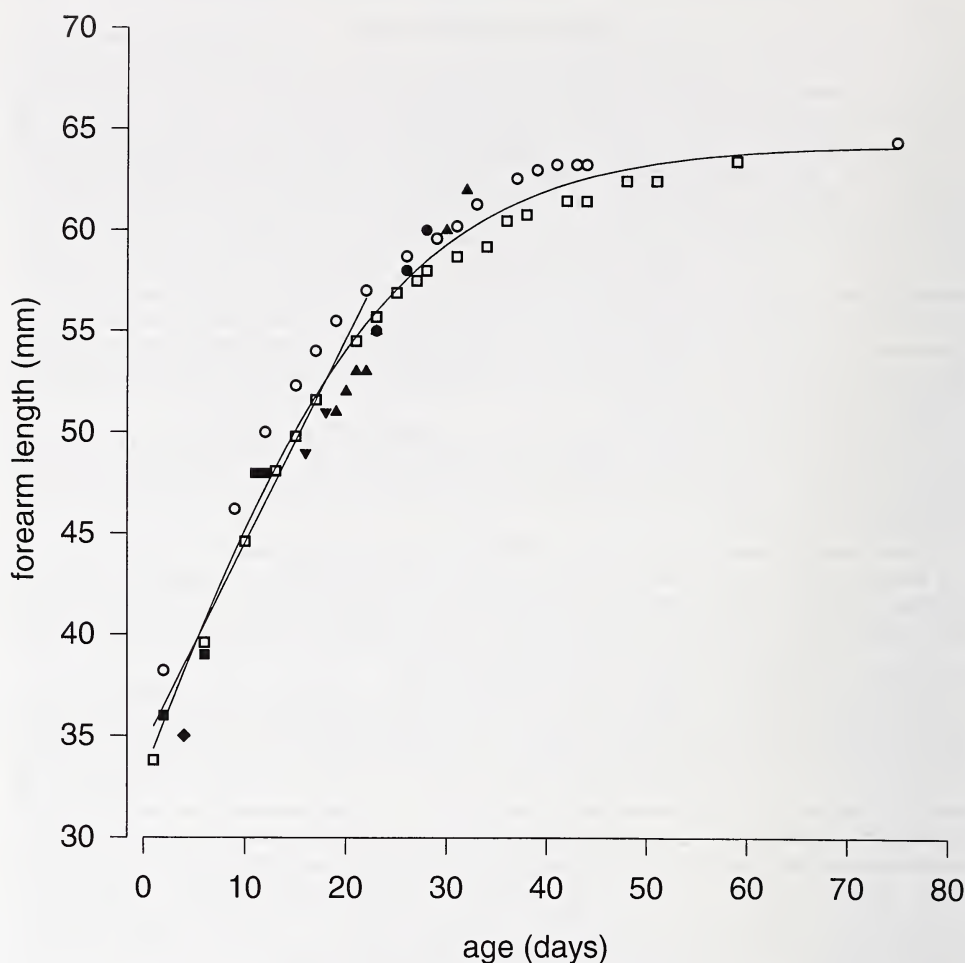


Fig. 1. Logistic growth model (forearm length = $64.382 \{e^{-0.080(\text{age}+0.697)} + 1\}^{-1}$), estimated using data of 2 captive (white symbols) and 5 free-ranging false vampires (black symbols). During days 1 to 22 growth almost follows a linear curve (forearm length = $1.008 \text{ age} + 34.455$).

'Parking' pups

Females carried their pups during flight even when the young had almost reached adult size (own observations; BROSET 1962). However, mothers also 'parked' their pup during night-time either in so-called night roosts ($N=4$) or in the day roost ($N=4$). Mothers leaving their pup in night roosts came to these roosts between 18.50 h and 19.10 h ($N=4$), probably immediately after they had left the day roost. They chose a roosting place and started to 'park' their pup. This procedure was complicated and took some time. First mothers landed at the ceiling and hung with the pup in carrying position. Then they made rhythmic and jerky movements with their muzzles towards the pup's rump ('muzzle-pushing') and bowed themselves ventrally towards the ceiling, probably to give the pup the opportunity to grip the roost's surface with its legs. During these bowing movements mothers spread their forearms. They had to bow up to 12 times until the pup clung to the ceiling. This behaviour included several bouts of jerky muzzle-pushing and

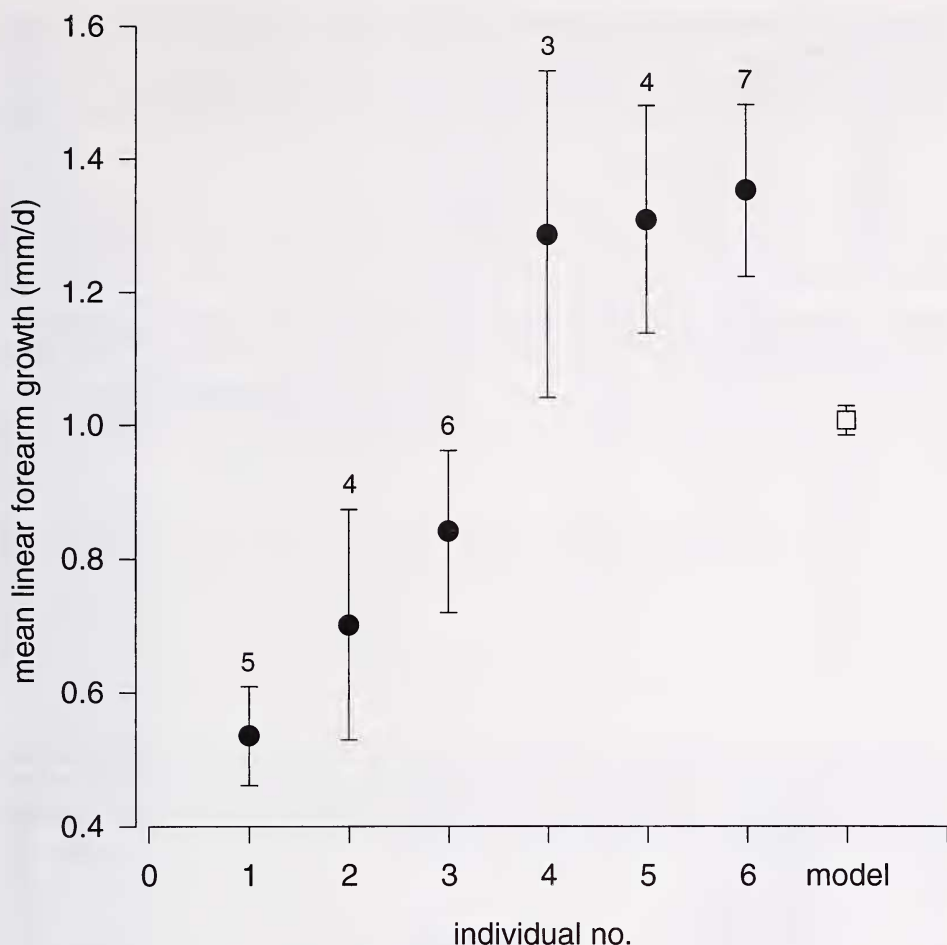


Fig. 2. Linear growth rates (\pm SD) of 6 individuals until day 22 compared with the linear proportion of the logistic growth curve from figure 1 (numbers refer to sample size on which the respective calculation is based).

bowing. The separation procedure lasted from 5 to 21 minutes ($N = 4$, median 9.75/8–10.5 min). Immediately after the pup had attached to the ceiling the mothers left the roost. Pups were left alone for 23% of the time, whereas 77% of the remaining time the mother joined it and the two hung together (Tab. 1). Mothers stayed in a night roost at least a minute and maximum 202 min ($N = 4$) and pups were on their own for at least 3 and maximum 170 min ($N = 4$). Detailed data were available for one mother in night roost 2: her median attendance interval was 83.5/18.5–151.5 min ($N = 12$) and her median absence interval was 39.5/30–59 min ($N = 10$).

Age at 'parking'

At what age did mothers 'park' their pups? If exact pup age was not known (5 cases) we estimated the age using the logistic forearm growth model. For three pups the exact age was known. Age of pups 'parked' for the first time inside the temple varied from 2 to

Table 1. Time (in minutes) mothers spent at and apart from the roosting site of their young (NR = night roost)

place	total time	mother present	mother absent
NR 1	244	173 (71%)	71 (29%)
NR 2	2 196	1 682 (77%)	514 (23%)
NR 3	90	90 (100%)	0 (0%)
NR 4	129	104 (81%)	25 (19%)
total	2 659	2 049 (77%)	610 (23%)

Table 2. Forearm length (in mm) and age (in days) of pups when they were 'parked' for the first time (NR = night roost, DR = day roost, F = female pup, M = male pup, * = age calculated using logistic growth equation, see figure 1)

location	pup	forearm length (mm)	age (d)
NR 1	F5	51	11
NR 2	M3	45	10*
NR 3	M4	56	23*
NR 4	F1	–	16
DR	M2	35	2*
DR	F2	53	19*
DR	F3	52	17*
DR	F4	36	3

19 days, median age was 10.5/2.5–18 days ($N = 4$, Tab. 2). Pups 'parked' for the first time in night roosts were 10–23 days old, their median age was 13.5/10.5–19.5 days ($N = 4$, Tab. 2). However, the age difference of pups 'parked' in temple and night roosts was not significant (Mann-Whitney U-test, $U = 10$, $p = 0.564$).

First flight

Twenty-seven days after the first birth had occurred, the first pup was fluttering inside the temple. From then on the number of flying pups increased to at least 4 until the end of the study period. However, so far no pup seemed to leave the day roost. One pup made its first flight attempts when its forearm was 58 mm long.

Two days later its forearm length was 60 mm. This was the last time the pup could be measured, since its increasing flying ability made further measurements impossible. In contrast, another pup hanging in night roost 4 did not make any attempts to fly when its forearm was 62 mm long. A third pup in night roost 3 could be recorded until its forearm measured 58 mm. The two captive bats from the laboratory colony (Munich, Germany) started to fly when their forearms were 60.5 mm and 62.6 mm long. Their respective ages were 35 and 30 days.

Contact calls

Contact calls of false vampires consisted of repeated squeaking sounds with a peak frequency of about 12 kHz (Fig. 3). A total of 107 contact calls was counted between February 9th and April 14th (Fig. 4). Then contact calls occurred so frequently that we stopped

counting them. Interestingly contact calls could be heard from the very onset of the study and hence 54 of all recorded contact calls (50.5%) occurred before a single pup was born (Fig. 4). Contact calls were not equally distributed throughout the day. A comparison of total observation time between February 9th and April 14th and the frequency of contact

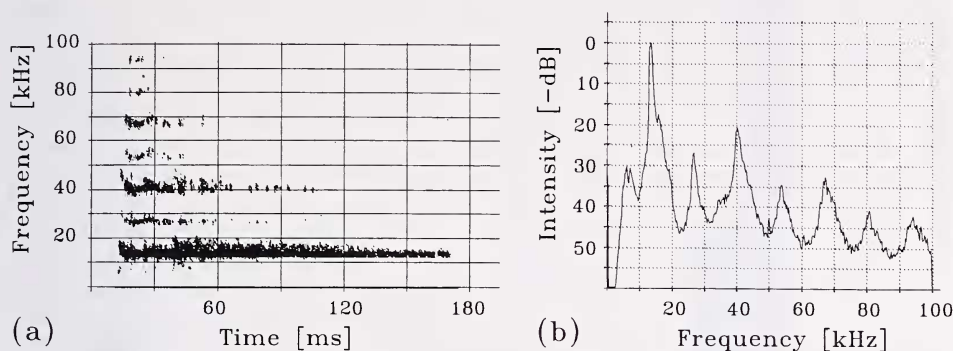


Fig. 3. Spectrogram (a) and sound spectrum (b) of a typical contact call of Indian false vampires.

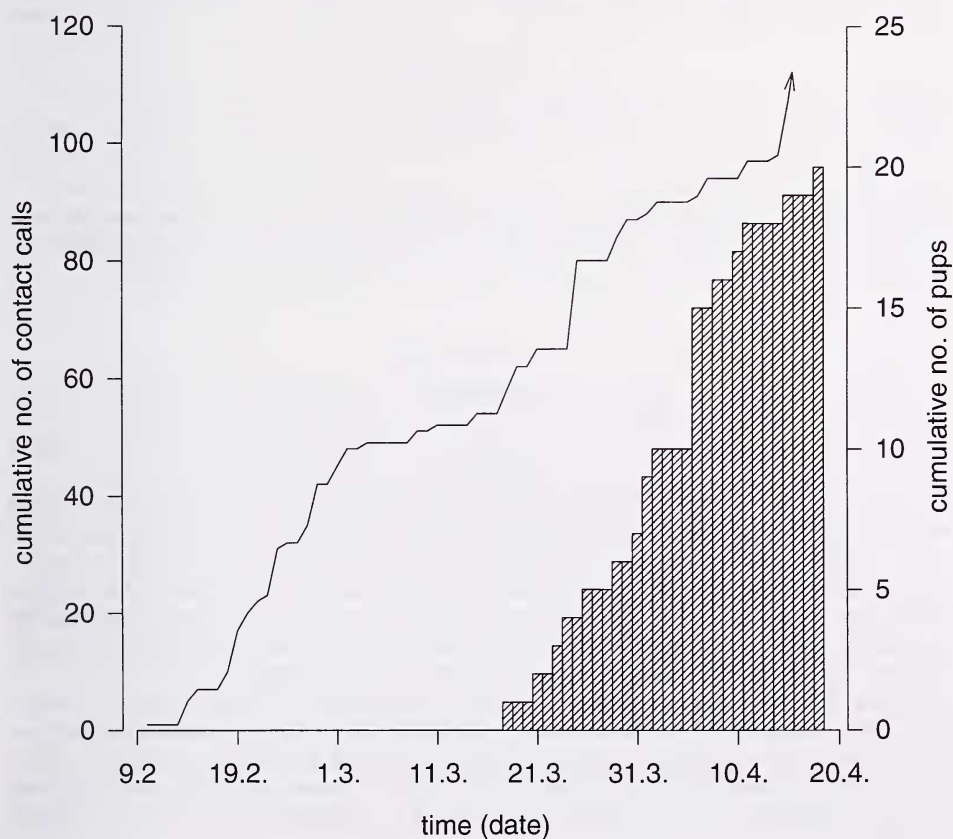


Fig. 4. Cumulative numbers of contact calls (line) and pups (bars) during the study.

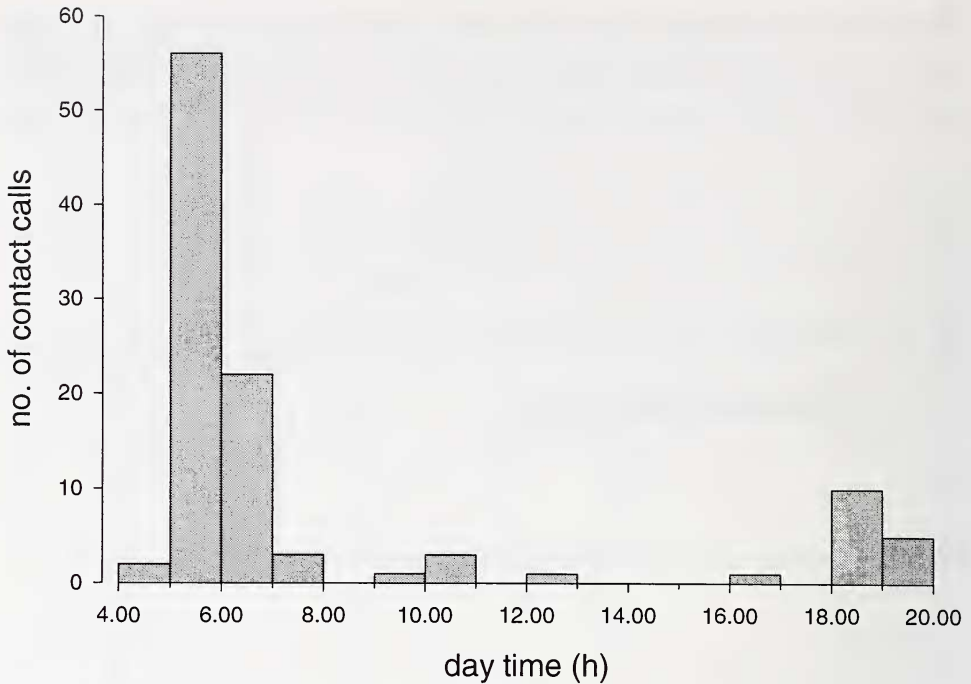


Fig. 5. Frequencies of contact calls at different times of the day.

calls revealed a significant difference (corrected Kolmogorov-Smirnov two-sample test, $N = 18$, $D = 0.444$, $p < 0.05$). The bats emitted contact calls more often in the morning during and after inflight (Fig. 5), when there were major movements in the colony.

Discussion

Parturitions

There are only few reports on parturitions in bats (WIMSATT 1960; KUNZ et al. 1994). Most microchiropterans appear to give birth by breech (feet first) presentation (KUNZ et al. 1994). Our observations support GOPALAKRISHNA et al.'s (1976) data that false vampires give birth head-first. Delivery by head first, however, may cause difficulties for the pup when trying to get into the carrying position, which is the same as already described for the closely related yellow-winged bat (*Lavia frons*; VAUGHAN and VAUGHAN 1987) and the African false vampire (*Cardioderma cor*; WICKLER and UHRIG 1969).

Births in 1995 occurred between March 17th and April 18th. Together with a study of BALASINGH et al. (1994) these data are in contrast with those of GOPALAKRISHNA and BADWAIK (1989), who suggested that parturitions of Indian false vampires throughout India occur within a narrow time window of 8–10 days in the second half of April. Also BROSET (1962) suggested a strict periodicity of Indian false vampires in a colony in Aurangabad.

'Parking' and growth

This study supports the findings of HABERSETZER (1983) who states that false vampire mothers always leave their pups in the same place within the day roost.

There was considerable variation in the age and developmental stage at which females began to 'park' their pups. Larger young, which were 'parked' in the temple for the first time at an approximate age of 17–18 days, could have been 'parked' at other places before. However, as mothers 'parked' pups in night roosts for the first time at an age of 10–23 days, it is likely that pups were 'parked' for the first time in the day roost at a similar age. One pup found alone in the temple was probably not older than one day. The temple provided constant temperatures of more than 30°C during day and night, whereas temperatures in night roosts most likely were subject to higher temperature fluctuations. Before 10 days of age pups are almost naked and may have problems to thermoregulate. As temperatures in night roosts were lower than in the day roost there might be a higher age limit for 'parking' pups in night roosts compared to the day roost, possibly explaining the lower variance in detachment age in night roosts. Growth rates of 2 pups parked in night roosts were relatively low, but the sample size was too low to be conclusive.

The overall variability in the onset of 'parking' could stem from differential maternal foraging abilities or prey preferences. In captivity mothers do not attempt to catch large prey like mice, when carrying a pup (LEIPPERT pers. obs.). Hence, mothers might adapt the onset of 'parking' according to their foraging skills or prey preferences. On the other hand, mothers rely on the cooperation of their pup, which has to attach to the ceiling of the respective roost. Hence, the variability in onset of 'parking' could also be the result of different outcomes of a parent-offspring conflict (TRIVERS 1974).

Forearm growth rates showed considerable variation between pups. Growth rates and survival of pups may depend on maternal age, rank, and body size (CLUTTON-BROCK 1991; HOFER and EAST 1996), as well as on ecological factors such as prey abundance (e. g. HOFER and EAST 1996) or, especially important in bats, on temperature (TUTTLE and STEVENSON 1982). Currently there is no information whether a reduced growth rate has fitness consequences for false vampires.

Usage of night roosts

Why do mothers carry their pups to night roosts instead of leaving them in the day roost? We found pups with forearm lengths of more than 60 mm in night roosts. The transport of such large pups must be a considerable effort for their mothers. This expenditure could possibly be balanced by energy savings due to shorter distances to the foraging areas. However, the distance from the day roost to the observed night roosts did not exceed 200 m. Furthermore, mothers spent most of the time roosting with their pups. Thus, the energy savings for mothers may be negligible. Alternatively, if mothers forage close to the night roost pups may be safer, as their mothers would be within calling distance. There is, however, some evidence suggesting that at least the foraging area of one mother was rather far (~750 m) from the night roost where the pup was "parked" (AUDET et al. 1991). Mothers spent most of the night roosting time (77%) with their pups. We were not able to collect data for non-lactating females and do not know whether the resting time of mothers exceeded those of other false vampires. Thus, it is unclear whether this species spends generally little time foraging or whether mothers maximise their attendance time.

Contact calls

Infants of numerous bat species emit isolation calls which allow a mother to identify her pup (e.g. FENTON 1977; GELFAND and McCracken 1986; THOMSON et al. 1985; ESSER and SCHMIDT 1989; SCHERRER and WILKINSON 1993). In the yellow-winged bat only mothers seem to call the pup (WICKLER and UHRIG 1969). Because in Indian false vampires both mother and pup used the same type of sound to contact each other we consider the term 'contact calls' more appropriate than the term 'isolation calls'. Contact calls were most frequently emitted in the morning when mothers returned to the roost and looked for their pup. Often after exchanging several such squeakings the mother flew to the pup or both met, when the pup was already volant (HABERSETZER 1983 and own observations). Since contact calls were also emitted before pups were born, it is likely that these calls do not only serve mother-pup recognition, but also other social purposes.

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Zusammenfassung

Geburt und Aspekte der Jungenaufzucht und -entwicklung bei Indischen Falschen Vampiren, Megaderma lyra

Dieser Bericht liefert die ersten Beobachtungsdaten zu Geburt und nachgeburtlicher Entwicklung von freilebenden Indischen Falschen Vampiren. Das Geschlechterverhältnis der Jungtiere war ausgeglichen und das Jungenwachstum, gemessen am Unterarm, folgte einer logistischen Wachstumskurve. Es zeigten sich jedoch große individuelle Unterschiede in der anfänglich linearen Wachstumsperiode (zwischen 0.53 mm/d und 1.35 mm/d). Als die Jungtiere zwischen 1 und 23 Tage alt waren, begannen Weibchen sie während der Ausflugsperiode im Tagesquartier oder in speziellen Nachtquartieren zurückzulassen. Mögliche Gründe für die Wachstumsvarianzen und die unterschiedlichen Zeitpunkte, ab wann die Weibchen ihre Jungen allein ließen, werden diskutiert. Kontaktrufe von Falschen Vampiren bestanden aus wiederholten Quietschlauten und wurden nicht nur von Weibchen und deren Jungen, sondern auch von anderen Tieren produziert. Kontaktrufe im Tagesquartier traten am häufigsten morgens und abends auf, wenn die Tiere entweder einfliegen oder sich auf den Ausflug vorbereiteten.

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